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A STUDY OF SYMPHYOGYNA ASPERA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 196

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(WITH PLATES XXX–XXXII)

The species of *Symphyogyna* are tropical and semitropical liverworts. They grow best in abundant moisture, and especially well in dripping water, but do not thrive in standing water. As a genus distinct from the other genera of Hepaticae, it was first described by NEES AB ESENBECK and MONTAGNE (9) in 1836, and four species were described: *S. brasiliensis*, *S. Hockstettii*, *S. difformis*, and *S. circinata*. Up to this time the first three species had been included in *Jungermanni*. The fourth species was evidently a new one. Additional forms were discovered, and later GOTTSCHE, LINDENBERG, and NEES AB ESENBECK (18) listed 24 species. SCHIFFNER (31), in his census of 1909, reports 27 species.

Symphyogyna is closely related to *Pallavicinia*, which is well known in our flora. These two genera have an interesting parallel series of plant bodies, ranging from the entire ribbon-like form to the deeply dissected and leaflike thallus which closely resembles a fern. While many of the species of *Symphyogyna* are distinctly anacrogynous in form, others with their leaflike lobes are strikingly like the acrogynous Jungermanniales, so that the genus as a whole holds a high rank among the Jungermanniales. Moreover, in the development of the sporophyte and the late differentiation of its sporogenous tissue, it almost approaches the condition of the mosses. STEPHANI (33) considers *Treubia insignis*, with its acrogynous characters, more closely related to *Symphyogyna* than to any other genus, and SCHIFFNER (31) places *Monoclea*, whose position among Jungermanniales has been severely contested by others, especially JOHNSON (22), close to *Symphyogyna*. These two relationships, whether real or imaginary, give some indication of the range of habit of the genus.

Comparatively little is known of the morphology of *Symphyogyna*. LEITGEB (26) gives a general survey of the genus and emphasizes in particular *S. sinuata*, *S. subsimplex*, and *S. rhizoloba*. He discusses the thallus, including the central strands of smaller cells, the apical cell, and the branches on the ventral side of the thallus. He passes over briefly the sex organs, giving no figures of the antheridia and few of the archegonia. He illustrates a close series of stages of the young sporophyte, but states that the later details in the development of the sporogenous tissue into spore mother cells and elaters remained dark to him. The only observations which he makes concerning the older sporophyte are that the apex of the sporophyte undergoes secondary divisions, to which is due the beaklike form of the tip of the capsule; that the differentiation into elaters and mother cells occurs relatively late; that the former are arranged in a direction parallel to the embryo axis and that they are uniformly distributed throughout the capsule. TANSLEY and CHICK (34) discuss more fully the structure of the central strand of the thallus. No other papers bearing directly on the morphology of the genus have been published, and only occasional references in connection with other liverworts have been made.

The highly developed conducting tissue of the gametophyte and the mosslike development of the sporophyte make the genus peculiarly interesting. It was hoped that a complete life history of the species might be secured, but many stages are lacking. While little is added to LEITGEB'S account, a few facts concerning a genus about which so little is known may be of interest.

Material

The material was collected in the vicinity of Xalapa and Texolo, Mexico, by Dr. W. J. G. LAND and Dr. CHARLES R. BARNES in the autumns of 1906 and 1908, and by Dr. LAND in the autumn of 1910. It was killed in the field in 6 per cent formalin made up with 50 per cent alcohol. Excepting for the young embryos, this killing agent was found to be satisfactory, and in fact it is almost a necessary one when time and light baggage are to be considered. From the alcohol-formalin solution the material was transferred to 50 per cent alcohol, and the process of dehydration was carried on through series of absolute alcohol and xylol into pure xylol, was imbedded in paraffin and cut, usually, 5 μ thick. Safranin and gentian violet, safranin and lichtgrün, and Haidenhain's iron-alum hematoxylin were the stains used.

Thallus

Symphyogyna aspera (figs. 1 and 2) has a rhizome-like portion which closely adheres to the soil, and from this rhizome arise somewhat inclined aerial branches. GOEBEL (15), in his description of *S. sinuata*, states that the winged shoots can again decrease at the apex and become stolons, but usually they conclude their growth after reaching a definite medium size, and then at their base they form a ventral lateral shoot which continues the growth as a stolon, subsequently rises above the substratum, broadens out, again forms a dorsiventral shoot, and so on. His illustration of *S. sinuata* shows a chain of five such generations. In *S. aspera* no indications were noted that the apex of the thallus may act as a stolon, but growth by a basal stolon is characteristic of this species also.

Rhizoids are very abundant, forming thick mats upon the ventral surface of the rhizome and parts of the aerial branches in contact with the soil. As has been previously noted, especially by BOLLETER (2) in *Fegatella conica* and by CLAPP (7) in *Aneura pinguis*, the ends of the rhizoids are curiously branched, twisted, and often greatly enlarged (figs. 3 and 4). The branched ends often tightly surround particles of foreign material. If there are cross-walls near the ends of the rhizoïds they must be quite rare, for none were observed in the material examined.

Fungi are abundant, especially in the rhizoids (figs. 5 and 6). A favorable view gave indications that the fungus had penetrated the tip of the rhizoid (fig. 6). The fungous species could not be determined from the preserved material, but evidently more than one species is present. Some hyphae are large and abundantly septate (fig. 5), and other hyphae are quite small, so that the septations, if present, could not be distinguished. Fungi have been frequently reported among liverworts, especially by LEITGEB (26), KNY and BOTTGER (24), J. PEKLO (30), GOLENKIN (16), NĚMEC (28 and 29), CAVERS (5), JANSE (21), GARJEANNE (13 and 14), and CLAPP (7). GARJEANNE has done an extensive piece of work in having examined over 30 species, and he concludes that the fungi neither do harm nor good to the host plant.

In transverse section, the rhizome of *S. aspera* is somewhat irregularly oblong (fig. 7). The cells are undifferentiated except in the central region, where there is a group of small, thick-walled cells which stand out in sharp contrast with the much larger, thinner-walled cells surrounding them. In longitudinal section they appear as very narrow, greatly elongated cells, whose pointed ends dovetail into each other (fig. 8). LEITGEB (**26**, p. 69) gives the length of the cells in *S. sinuata* as 0.3 mm. and the breadth 0.009 mm. In *S. aspera* the cells are 0.537 mm. long and 0.008 mm. in diameter.

The aerial part of the thallus has the same general structure as the rhizome (fig. 9). There is a central region of small, thick-walled cells surrounded by broader, thin-walled cells, which together form the midrib of the thallus. From the midrib the thallus narrows abruptly into winglike extensions consisting of one layer of cells. By treating the thallus, either the rhizome or aerial parts, with Schulze's macerating solution, the cells of the central area can be separated entire, and by staining them with Delafield's hematoxylin, the structure of the cell walls may be seen distinctly (fig. 10). This treatment enables one to get a more accurate measurement of their length, and it is also interesting to know that they remain intact after the action of this reagent. The cells of the wing are disintegrated, but some cells surrounding the central strand may remain intact provided the action of the reagent is not too long (fig. 8). These long, narrow cells, with their thick walls and spirally arranged pores, make *Pallavicinia*, *Hymenophyton*, and *Symphyogyna* peculiarly interesting. They were discovered by Sir WILLIAM HOOKER in 1816 in *Pallavicinia Lyellii*. In 1864 GOTTSCHE (17) described them in *S. sinuata*. LEITGEB (**26**, p. 69) describes the cells with their spirally arranged pores, but he has no illustrations. FARMER (10) adds little to LEITGEB'S account, though he gives a good drawing of the transverse section of the rhizome, and also one showing the lack of continuity between the strand of the main part of the thallus and that of the ventral branch. TANSLEY and CHICK (34) discuss fully the strands in *Pallavicinia*, *Hymenophyton*, and *Symphyogyna*, and they have demonstrated with eosin that in *Pallavicinia Lyellii* the strands conduct water. Their detailed drawing of part of a cell showing pores (*pl. 1. fig. 4*) is representative of the pores in *Symphyogyna*, with the probable exception that in *S. aspera* the pores are more regularly arranged and more obliquely spiral. Sections of the thallus treated with acidulated alcohol and stained with methylene blue, following Mayer's method given by HAAS and HILL (19), gave the test for pectose by showing the middle lamella stained a deeper blue (fig. 11). The pores are so narrow that except in very thin sections they are readily overlooked in transverse sections.

In the species of *Symphyogyna* which he examined, LEITGEB found the dolabrate apical cell like that in *Pallavicinia*, etc., though for *S. sinuata* he makes the statement that at first glance one might think the apical cell like that in *Pellia calycina*, *Blasia*, etc., which is the well known wedge-shaped cell. However, he considers that such a view is an erroneous one, and that the apical cells of all the species of *Symphyogyna* are alike. *S. aspera* has two types of apical cell, the dolabrate and the wedge. STEPHANI identified the species and grateful acknowledgments are due him. However, in the material sent to him, the part collected at Texolo, Mexico has the wedge-shaped apical cell, and that collected at Xalapa has the dolabrate apical cell. Moreover, the thallus of the material collected at Texolo is slightly broader and less deeply lobed than the material collected at Xalapa. The last two characters may be overlooked as due to a difference in environment; but when to them is added a difference in the apical cell, one may be justified in considering the material as representing different species, especially since species are often separated for less convincing reasons. If both forms belong to the same species, then there is the interesting situation of two types of apical cell in mature plants of the same species (figs. 12–16). However, CAMPBELL (3) reports two types of apical cell in *Calycularia radiculosa*.

In the dolabrate cell a segment is cut off alternately to the right and left. The primary segments on both sides are divided longitudinally, and from the middle secondary segment in each side can be traced the one-layered winglike extensions of the thallus (fig. 17).

From the nature of the dolabrate apical cell there cannot be true dichotomy, if by the term "true dichotomy" is meant the division of the apical cell into two segments alike in shape and size and also like the original apical cell. This seems to be the only standard for the determination of true dichotomy; but frequently the organization of the apical cell of the branch occurs so close to the apical cell of the main branch that the mature thallus has the appearance of true dichotomy. In the liverworts which have a wedge-shaped apical cell true dichotomy is the probable form of branching; for a cell of this form can be divided into two cells which are alike in size and shape and also like the parent cell; although it is possible that segments near the apical cell may organize a new apical cell.

Two-celled mucilage hairs are organized from segments close to the apical cell, and these occur on both the dorsal and the ventral sides. These mucilage hairs at first project over the apical region of the thallus; but as the thallus grows new ones are formed and the older ones, apparently in good condition, can be seen far back from the apex. LEITGEB (26, p. 73) states that they are more abundant on the ventral than on the dorsal side of the thallus, and this statement seems to be true also for *S. aspera*. The mucilage hairs are formed only in the immediate vicinity of the apex.

Branching on the ventral side of the thallus of *S. aspera* is quite common. LEITGEB discusses rather extensively the situation, and traces the branches close to the apical cell.

Sex organs

Symphyogyna is dioicous, the plants bearing antheridia usually being more slender than those bearing archegonia.

ARCHEGONIA

The archegonia are borne in groups in the dorsal side of the thallus. Each group is surrounded by a deeply dissected involucre, which is attached on one side to the thallus. Usually there is a group at the place of forking of the thallus, but they are not restricted to that region, and often there are several groups close together on one branch. The archegonia have their origin close to the apical cell (fig. 18), and in this particular thallus the initial shown is the only one of the group which had made its appearance. Moreover, a cell which would have been actively involved in the development of the involucre is in the second row to the left of the initial. Since similarly shaped cells may be distinguished in several sections, it seems probable that the involucre has its origin from a row of meristematic cells. As the archegonia (figs. 19–25) develop, the thallus below them becomes meristematic, so that the archegonia come to be arranged on a pad, as is common among the anacrogynous Jungermanniales.

The earliest stage of an archegonium might readily be mistaken for a young mucilage hair; but a mucilage hair may be distinguished by the bend which it makes very early toward the apical cell. By transverse divisions the archegonial initial is divided into a tier of three cells, and the outermost cell by three longitudinal walls is divided, in the usual way, into four cells, an inner cell surrounded by three outer cells (fig. 21). The neck of the archegonium is long, and the neck cells are spirally arranged, as in the mosses (fig. 6). There were counted 13 neck canal cells in one archegonium, and in another archegonium the neck canal row was in part double (fig. 28). The egg is small, and in that respect it resembles the egg of mosses. An undoubted case of fertilization was not seen, though fig. 27 represents an archegonium which may be interpreted as showing fertilization. The withered neck cells and the presence of young embryos in the same cluster add weight to this interpretation.

ANTHERIDIA

The antheridia are grouped in compact masses on the midrib on the dorsal side of the thallus, and each antheridium is surrounded by a small involucre somewhat similar to the one which surrounds each group of archegonia. (Spruce 32, *pl. 30*), in a diagrammatic way, illustrates the antheridial scales of *S. trivittata*. More than one group of antheridia may occur on the same thallus, indicating a cessation followed by a renewal of activity in the production of antheridia. This feature Leitgeb observed in the species which he investigated (26, p. 74). No plants bearing antheridia were found in the material which gave the young stages of archegonia, and though many antheridial plants were mixed with the plants bearing sporophytes, the antheridia with few exceptions had discharged their sperms and fallen off. The few antheridia that were found seem to have been delayed ones. No very young stages were obtained, but the older ones indicate the method of development usual in the Jungermanniales (figs. 29–31). The body of the antheridium is nearly spherical, and the stalk is short and slender.

Sporophyte

The fertilized egg is divided into two cells by a transverse wall (fig. 32), and a third cell is cut off by a wall parallel to the first. In the material studied karyokinetic figures were entirely lacking in the young embryos, so that it is impossible to state with certainty whether it is the epibasal or hypobasal cell that divides. LEITGEB mentions that in *S. rhizoloba* it is the inner cell which remains undivided, and that this cell can be recognized in well developed embryos. He gives a close series of stages for this species, and apparently after the row of three cells is formed there is some variation in the subsequent walls. However, he states that the outermost cell is divided by an oblique wall. This may also be true for *S. aspera* (fig. 33). This oblique wall is the beginning of the apical growth which LEITGEB emphasizes very strongly for *S. rhizoloba*, and in fact later stages of *S. aspera* (figs. 35–37), with their marked segmentation, seem to verify this method of development.

The young embryo is slender, and it is early shown that the uppermost part is the region most actively involved in cell division, and that part is also marked by a denser cell contents. The middle part is concerned with elongation, and there the cells lengthen, with little activity in cell division (fig. 37). The cell contents in this part is less dense than in the upper part, and it is also greatly vacuolate. The innermost cell of the embryo may very early divide, as shown in fig. 34, but, judging from the general contour of the young embryos and without the aid of figures, it seems probable that cell multiplication in this part of the embryo is restricted to very few divisions. Periclinal walls are formed separating the amphithecium from the endothecium. Three wall layers are formed, the middle layer being apparently cut off from the outer layer (fig. 38). The walls of the outermost layer of cells thicken as the sporophyte matures, and the two inner layers do not entirely disappear, so that the mature capsule wall is not one layer thick, as has been reported for some species of *Symphyogyna* (1). Plastids are quite numerous in the cells of the capsule wall. The beaklike extension of the apex of the capsule is prominent, as LEITGEB noted in the species which he studied (fig. 38). The foot of the mature embryo is often somewhat anchor-shaped, but more frequently there is a gradual narrowing toward the tip of the foot, which is always bent over in a mosslike manner (fig. 39). The cells of the thallus surrounding the sporophyte become greatly disintegrated, and the foot of the mature sporophyte is imbedded in a mucilaginous mass. The pad upon which the archegonia stand elongates as the embryo grows, and the non-functioning archegonia are carried up to the apex of the calyptra. Five young embryos were found in one group, and it is quite common to find two or three together. The potentially sporogenous cells are sharply delimited from the beginning by their denser cell contents, larger nuclei, and active cell division.

SPORE MOTHER CELLS

The subsequent history of the sporogenous part of the embryo is interesting and important, for there must be a fundamental process which lies back of the formation of the curiously lobed spore mother cell so uniformly characteristic of the Jungermanniales. In the Marchiantiales it is a simple matter to dismiss the formation of the spore mother cells with the familiar expression that they "round up"; but the formation of a lobed mother cell demands more consideration. However, the stages immediately preceding the rounding up of the mother cells in the one group, and the lobing of the mother cells in the other group, are fundamentally the same. These stages in permanent mounts show the sporogenous cells irregular in shape, and bearing every indication that they were plasmolyzed in the fixation or imbedding. As mentioned above, LEITGEB frankly admits that he did not understand the processes leading up to the formation of the spore mother cells and elaters; and KIENITZ-GERLOFF (23), in discussing the Jungermanniales, adds nothing of importance. While a great deal has been written on the mitoses in the spore mother cell, literature on the formation of the mother cell is strikingly scanty. LECLERC DU SABLON (25) has made some important observations. He carefully investigated the development of the sporophyte of *Frullania dilata*, and with that species he compared *Scapania compacta*, *Pellia epiphylla*, *Aneura pinguis*, *Targionia hypophylla*, and *Sphaerocarpus terrestris*. He emphasizes some important points, namely, that there is an early differentiation between elaters and spore-producing tissue; that the elater is the equivalent of a row of mother cells; and that the walls between spore mother cells and elaters early become gelatinized. In the following statement he considers the irregularity of the potential spore mother cells, but does not seem to consider this feature of any importance.

> Tandis que certaines masses protoplasmic (*s*) destinées à devenir cellules-mères de spores s'accroissent régulièrement sur tout leur pourtour et présentent l'aspect d'amibes à peu près isodiamétriques d'autres (*el*) s'allongent exclusivement dans une direction, et acquièrent la forme se produit cet accroissment rapide, si c'est par formation de cellules nouvelles, ou par l'elongation des cellules déjà existantes.

Again he says (25, p. 169):

> Les cellules-mères continent a s'accroitre pendant longtemps encore, puis on voit apparaître à leur surface de petits sillons, premier indice d'une division en quatre spores. Pendant que ces sillons se creusent et accusent ainsi de plus en plus la forme de tétrade que prend la cellule, le noyau se divise en quatre, puis le protoplasma se divise de même, et à partir de ce moment on peut dire que la division de la cellule-mère en quatre spores est consommée, les phénomènes qu'on observe ensuite étant d'un ordre tout a fait accessoire.

CAMPBELL (4, p. 111) does not agree with LECLERC DU SABLON'S observations on the disappearance of the walls in the sporogenous tissue, and in this connection he makes the following statement:

> A great many carefully stained microtome sections of a large number of liverworts belonging to all the principal groups have been examined by me and invariably the presence of a definite cell wall could be demonstrated at all stages.

Again, he says (4, p. 34) in regard to the Ricciaceae:

> As the sporogonium increases in diameter, the central cells begin to separate and round off. Their walls become partially mucilaginous and in microtome sections stain strongly with Bismarck-brown or other reagents that stain mucilaginous membranes. With this disintegration of the division walls the cells separate more and more until they lie free within the cavity of the sporogonium.

FARMER (10), in discussing *Pellia epiphylla*, says in regard to the spore mother cell:

> At first more or less irregularly spherical, it soon becomes four-lobed, and these lobes increase in size, chiefly owing to radial extension, so that the spore mother cell ultimately comes to consist of four large sacs whose cavities communicate with each other by means of a small central space common to them all.

In a later paper (11), in summing up the characteristics of the sporogenous tissue of the Hepaticae, he says:

> A third feature of some interest, and which in practice is especially noticeable, is that just at the period of the spore-formation it becomes exceedingly difficult to fix the cells without some contraction. This is the more remarkable since the nuclei, which may happen to be dividing in either earlier or later stages, present not the slightest difficulty. Moreover, the cytoplasm also stains deeply with most nuclear stains, and everything points to the conclusion that there is something going on in the cell during this so-called reduction division which is not met with at any other period, whether in resting or dividing cells.

WILSON (34), in regard to *Mnium hornum*, says:

> FARMER has already noted that at the reduction division the spore mother cells of the Hepaticae can only be fixed with great difficulty. This is especially the case in the Muscineae.

Of the spore mother cell of *Pallavicinia decipiens*, FARMER (10) says:

> The mother cell becomes tetrahedrally lobed, and the cell walls at their inner angles grow into the cell cavity towards the nucleus.

These citations are representative of the literature on spore-formation in the Hepaticae.

While the spore mother cells of *Symphyogyna* are comparatively small, the large amount of sporogenous tissue in each sporophyte and the deep lobing of the mother cells make it a favorable species for study. A young sporophyte, such as is represented in part by fig. 40, shows no differentiation in the sporogenous tissue, though some of the longer cells may be considered as potential elaters. In an older sporophyte (fig. 41) the elaters by their elongation are in sharp contrast with the cells which will produce spore mother cells. In such a sporophyte the protoplasts have contracted slightly from the cell walls, which are still distinctly seen, and the intervening spaces are filled with a mucilaginous substance which stains a faint yellow in gold orange. The protoplasts show no difference in their staining, and excepting the difference in shape are alike in general structure. In older sporophytes (fig. 42) the elaters have assumed their characteristic shape, and their protoplasts are undergoing the peculiar changes incident to the formation of the spiral thickenings. The walls between the cells are still distinct, but they have lost some of their sharpness, and the mucilaginous substance stands out more distinctly when stained with gold orange. The pronounced irregularity of the shape of the cells which are to produce spore mother cells is a striking feature, and this irregularity continues until the lobed mother cell is fully mature. From the beginning of the differentiation of elater-producing cells and sporogenous cells (fig. 43), the division of the sporogenous cells continues, and frequently lobed mother cells and sporogenous cells still in division are seen in the same capsule.

Since living material of *Symphyogyna* could not be obtained to verify the observations made from prepared slides, *Pellia epiphylla*, *Aneura pinguis*, *Pallavicinia Lyellii*, *Cephalozia bicuspidata*, and *Porella platyphylla* were studied. The sporogenous tissue was separated from the walls of the sporophyte and mounted in water, and also other material was studied in the crushed sporogonium without the addition of any reagent whatever. The living cells were immediately examined under the microscope, and they were found to show the same irregular amoeboid forms which had been noted in the permanent mounts. Sporophytes from the same material were killed in different strengths of chromo-acetic, with and without osmic acid, and in Benda's solution, and in each case the results showed the same irregularity of the sporogenous cells (figs. 56–60). Moreover, in the laboratory all slides of sporophytes of liverworts belonging to the Marchantiales, Jungermanniales, and Anthocerotales, in the stages preceding the maturity of the spore mother cell, show the same situation. These slides are the accumulation of years and have been made by different people. On account of the lobing of the mother cell, the Jungermanniales show the irregularity to a more marked degree and for a longer time, but before the rounding up of the mother cell in the other groups, similar irregularity in shape and peculiarity in staining may be seen. From the observations made, it may be a reasonable interpretation that during the development of the tissue which eventually gives rise to spore mother cells, the protoplasts assume amoeboid forms, and the walls undergo a change. Older stages of the sporophyte (figs. 42–44) show increase in the accumulation of the mucilaginous substance and also the reducing of the cell walls into a substance of that nature. HOFMEISTER (**20**, p. 81) notes that the walls become considerably thicker, and that the substance of these walls is converted into a substance which swells extensively in water. There are striations which readily could be mistaken for walls, but any mucilaginous substance may give that effect.

Development of the spore mother cells in an individual sporophyte is not simultaneous, as may be seen in fig. 44, which shows the beginning of the lobing of one mother cell and other sporogenous cells still dividing. As the mother cell begins to become lobed, the extensions of the protoplast become more marked and vacuoles seem to play an important part in the process of lobing. A characteristic stage (fig. 45) shows the orientation of the four lobes and in each lobe there is a large vacuole. Later (figs. 46 and 47) the large vacuoles are broken up into smaller ones and the cytoplasm is uniformly distributed throughout each lobe. Apparently the nucleus always occupies the central position of the mother cell.

DAVIS (**8**), in discussing the spore mother cell of *Anthoceros*, asks the question whether the cytoplasm could be intrusted with so important a task as the preparation of a chloroplast for each of the four nuclei. A similar question may be asked in regard to the lobing of the mother cells. In the lobing of the mother cells it seems as if there are two alternatives: either the nucleus, long before it shows any visible signs of activity, affects the cytoplasm to such a degree that the four lobes are organized in advance of the reduction division of the nucleus; or the cytoplasm, in addition to the nucleus, is an important factor in the reduction division.

The quadripolar spindle may be distinctly seen at the beginning of the reduction division (fig. 51); but the later stages (figs. 52 and 53) verify MOORE'S interpretation (27) rather than the interpretation of FARMER (10). The chromosomes are very short and thick (fig. 48).

The four young spores gradually separate (fig. 51). At this stage of the sporophyte the greatly elongated nuclei of the elaters, with their strong bands of chromatin and prominent nucleoli, are very striking. The mature spore (fig. 55) measures about 18.3 μ in diameter. The echinations are short but very sharp, and a surface view (fig. 53) shows them distinctly reticulate. Spores with two nuclei (fig. 54) are not very common, but enough were found to lead one to think that there is a feeble tendency toward intrasporal germination. The mature elaters (fig. 55) have two very prominent spirals.

Summary

1. The thallus of *Symphyogyna aspera* has a central strand of greatly elongated cells which taper at both ends. The walls of these cells have narrow pores which are spirally arranged.
2. Like the other species of the genus, *S. aspera* is dioicous. The plants bearing antheridia are more slender and less freely branched than the plants bearing archegonia.
3. The antheridia are scattered over the thickened part of the thallus on the dorsal side. Each antheridium is surrounded by a scale.
4. The archegonia are in groups on the dorsal side of the thallus. Each group is on a padlike extension of the thallus and is surrounded by an involucre.
5. More than one embryo may be formed in a group, but so far only one has been found to reach maturity.
6. As the embryo elongates, the calyptra and pad also elongate and the old archegonia are left in the tip of the calyptra.

7. The young embryo develops by segmentation similar to that formed by a dolabrate apical cell.

8. The sporogenous tissue is differentiated relatively late in the history of the sporophyte.

9. The cells which are to form elaters may early be distinguished from the cells which are ultimately to give rise to the spore mother cells. The former cells elongate without further division, while the latter cells undergo several divisions.

10. The walls of the sporogenous mass of cells become gelatinized, and the protoplasts are potentially free in the gelatinous substance.

11. The spore mother cells attain their lobing by a slow amoeboid change of the protoplast, and in this movement vacuoles seem to play an important part. The examination of the living sporogenous tissue of other Jungermanniales verifies the occurrence of this phase in them also.

12. Spores with two nuclei have been found, though this is not a usual condition.

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EXPLANATION OF PLATES XXX–XXXII

Symphyogyna aspera

FIG. 1.—Thallus with antheridia; ×2.

FIG. 2.—Thallus with sporophytes; ×2.

FIGS. 3, 4.—Ends of rhizoids; ×700.

FIG. 5.—Rhizoid containing a septate fungus; ×700.

FIG. 6.—Tip of rhizoid showing a fungus; ×1600.

FIG. 7.—Transverse section of rhizome; ×70.

FIG. 8.—Outline of a longitudinal view of a cell from the central region and three adjoining cells; ×180.

FIGS. 9, 10.—Cells of thallus adjoining cells of central region; ×180.

FIG. 11.—Transverse section of aerial part of thallus; ×170.

FIG. 12.—Part of cell of central region showing pores; ×2300.

FIG. 13.—Transverse section of cells of central region; ×1300.

FIG. 14.—End view of apical cell; ×645.

FIG. 15.—Section of apical cell parallel with the surface of the thallus; ×645.

FIG. 16.—Median longitudinal section of apical cell; ×645.

FIG. 17.—Median longitudinal section of wedge-shaped apical cell; ×645.

FIG. 18.—Transverse section of wedge-shaped apical cell; ×645.

FIG. 19.—End view of apical cell showing segment from which the wing has its origin; ×645.

FIGS. 20–22.—Stages in the development of the antheridium; ×700.

FIG. 23.—Median longitudinal section of thallus showing apical cell, initial of archegonium, beginning of involucre, and beginning of development of central cells; ×645.

FIGS. 24–30.—Stages in the development of the archegonium; ×645.

FIG. 31.—Archegonium showing spiral arrangement of neck cells; ×140.

FIG. 32.—Archegonium showing probable fertilization; ×1300.

FIG. 33.—Archegonium showing a doubling of the neck canal cells in one part; ×645.

FIGS. 34–38.—Stages in the development of the embryo; ×645.

FIG. 39.—Older stage of embryo; ×450.

FIG. 40.—Another view of the basal part of the embryo shown in fig. 39; ×450.

FIG. 41.—Tip of mature sporophyte; ×180.

FIG. 42.—Foot of mature sporophyte; ×180.

FIG. 43.—Part of young embryo showing sporogenous tissue and walls, and length of sporogenous tissue; ×860.

FIG. 44.—Part of sporogenous tissue showing the beginning of contraction of protoplasts; ×860.

FIGS. 45–47.—Stages in development of sporogenous tissue; ×860.

FIG. 48.—Early stage of lobing of mother cell; ×1600.

FIG. 49.—Late stage of lobing of mother cell; ×1600.

FIG. 50.—Mature spore mother cell; ×1600.

FIG. 51.—Mature spore mother cell just before reduction division; ×1600.

FIG. 52.—Spore mother cell during reduction division; ×1600.

FIG. 53.—Homotypic division of spore mother cell; ×1600.

FIG. 54.—Young spores nearly separated; ×1600.

FIG. 55.—Surface view of echinations of spore coat; ×1600.

FIG. 56.—Mature spore; ×1600.

FIG. 57.—Mature spore with two nuclei; ×1600.

FIG. 58.—Mature elater; ×1600.

Pellia epiphylla

FIG. 59.—Outline of spore mother cell from living material; ×1300.

Aneura pinguis

FIGS. 60–64.—Outlines of sporogenous cells from living material; ×1300.

FIGS. 65–67.—Outlines of sporogenous cells from preserved material; ×1600.

Pallavicinia Lyellii

FIGS. 68–75.—Outlines of sporogenous cells from living material; ×1300.

FIGS. 76–83.—Outlines of sporogenous cells from preserved material; ×1600.

Cephalozia bicuspidata

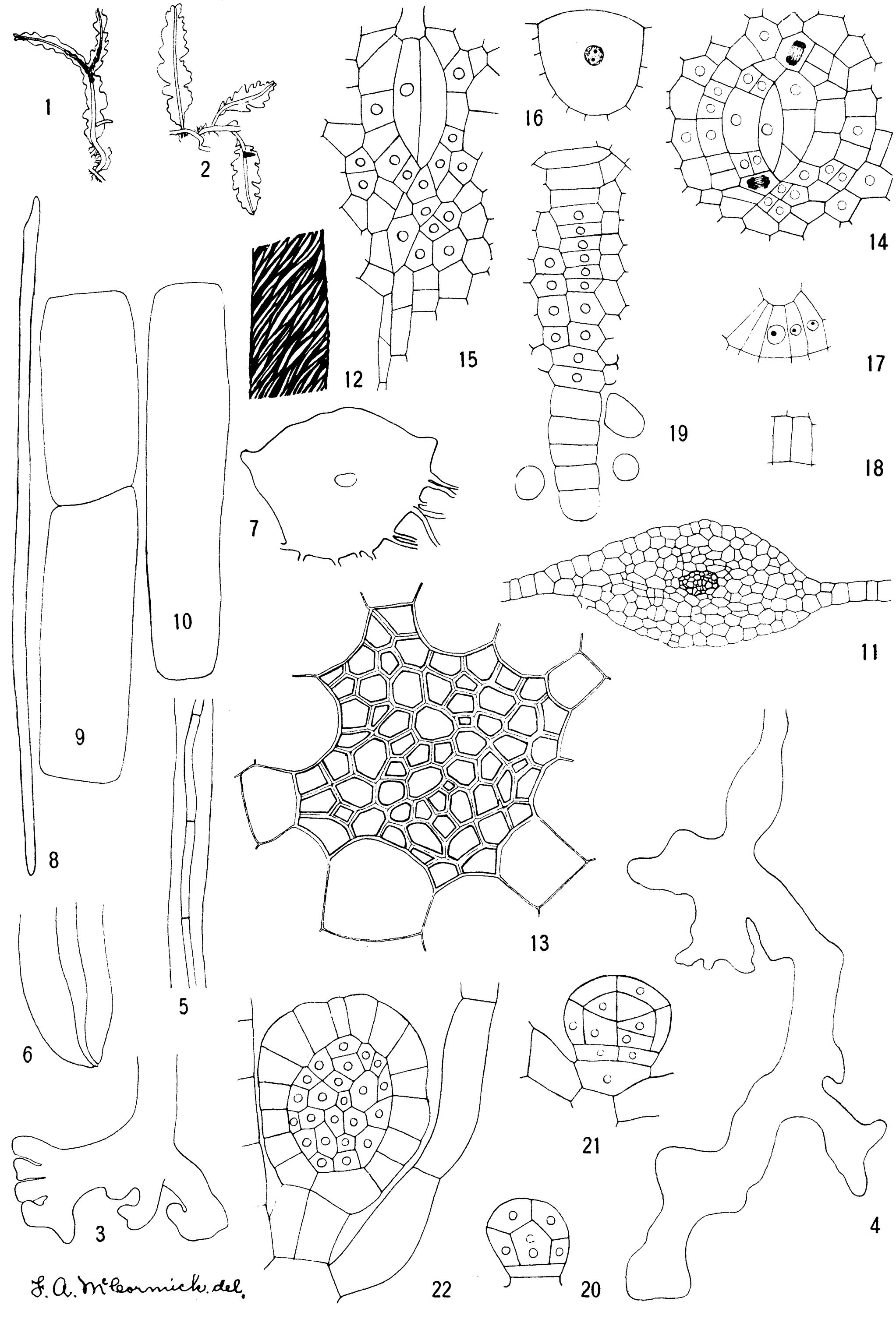
FIGS. 84–87.—Outlines of spore mother cells from living material; ×1300.

FIGS. 88–93.—Outlines of spore mother cells from preserved material; ×1600.

Porella platyphylla

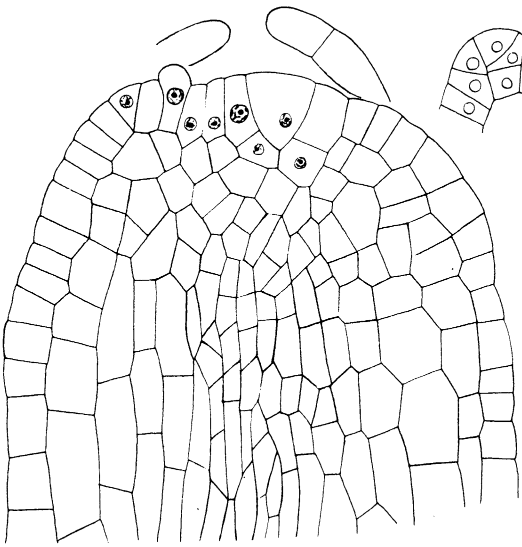
FIGS. 94–99.—Outlines of spore mother cells from living material; ×1300.

FIGS. 100–102.—Outlines of spore mother cells from preserved material; ×1600.



L. A. McCormick. del.

McCORMICK on SYMPHYOGYNA



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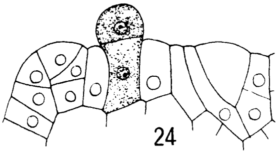

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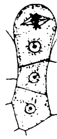

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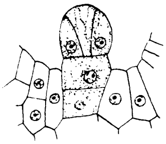

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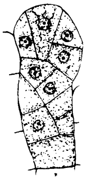

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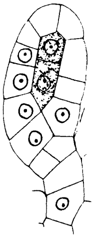

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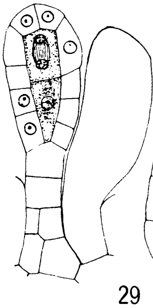

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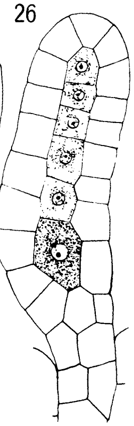

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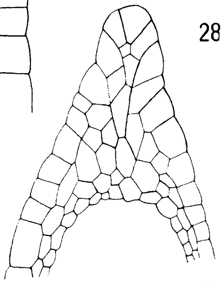

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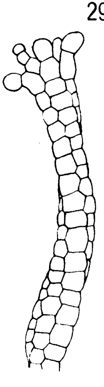

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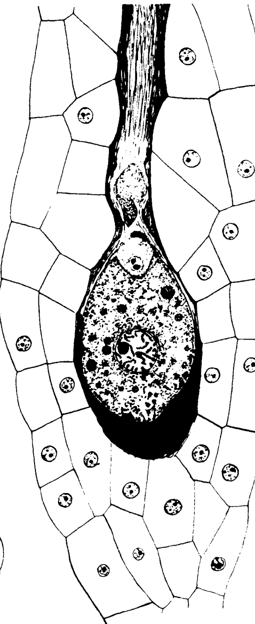

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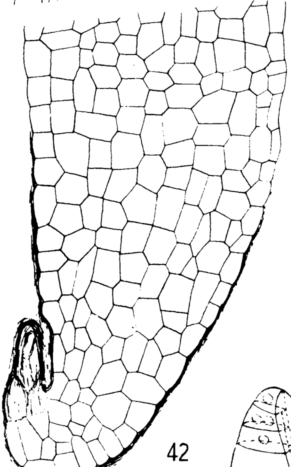

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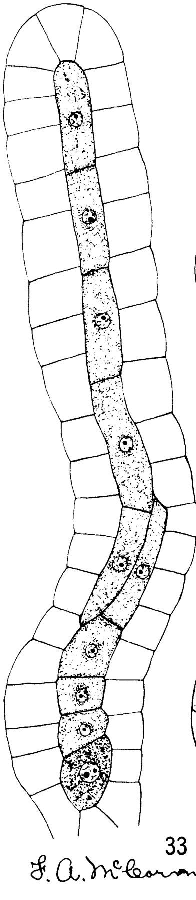

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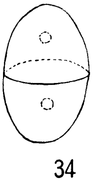

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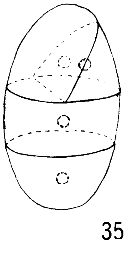

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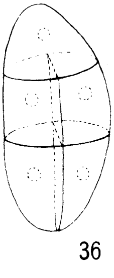

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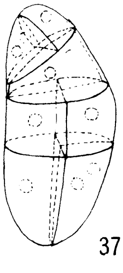

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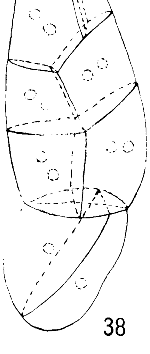

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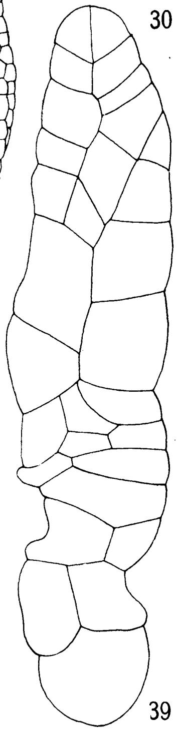

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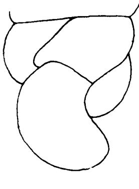

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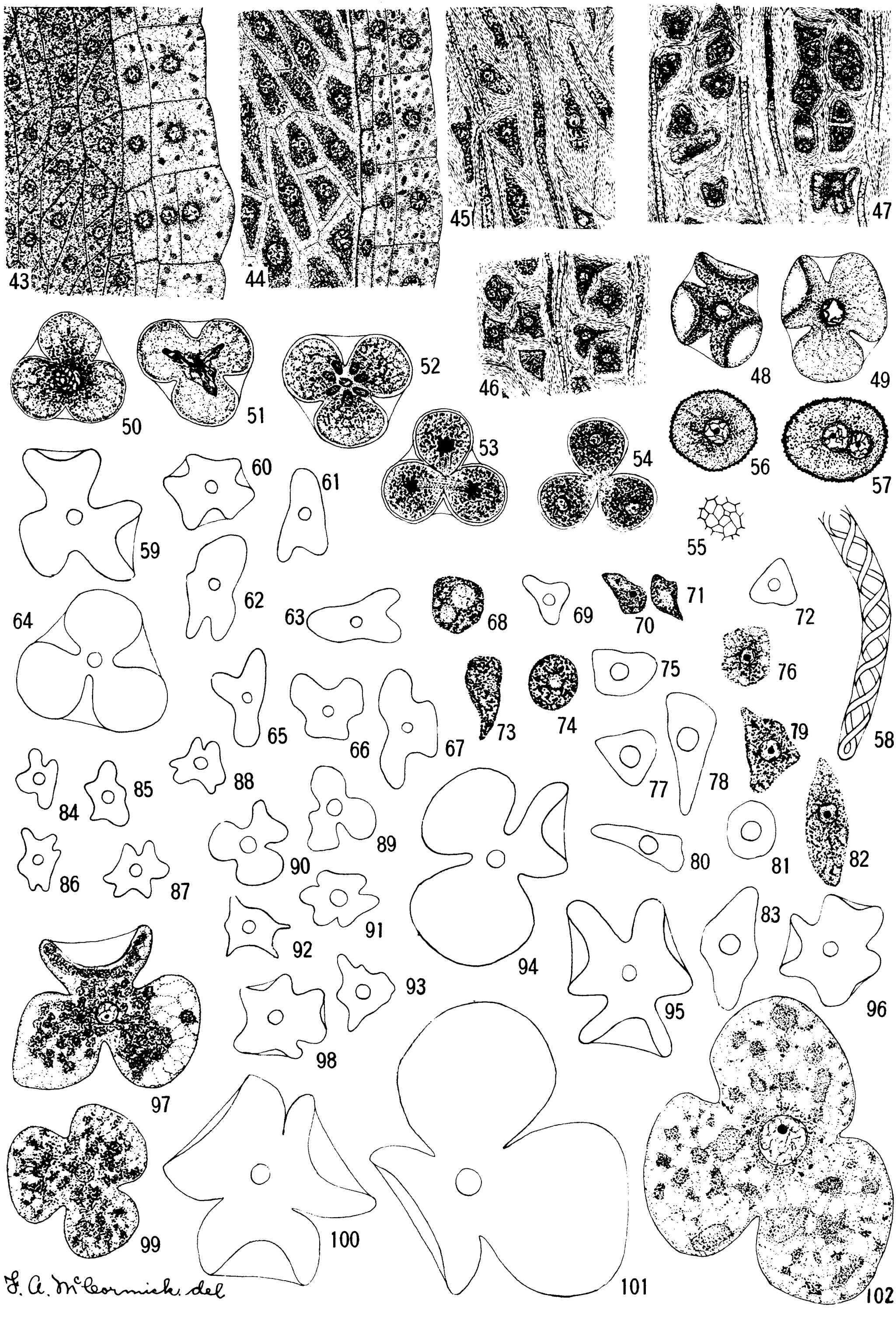

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